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## Evolution of Xylem Lignification and Hydrogel Transport Regulation

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*We have mapped the micron-scale distribution of cell-wall compounds in water-conducting cells with x-ray microscopy and shown that it varies across vascular plants. We have also shown that the extent to which water-transport properties can be modified by changes in the ionic content of transported water correlates with wall chemistry, which is consistent with the proposed wall-chemistry-based mechanism for this hydraulic response. Thus, the distribution of two key cell-wall compounds — hydrophilic polysaccharides and hydrophobic lignin — can likely affect the hydraulic and mechanical properties of cell walls. The evolutionary diversification of vascular cell types may reflect biochemical innovations evolved to fulfill opposing transport and structural support functions.*

All land plants have primary cell walls that are largely made of polysaccharides, such as cellulose and pectin. The water-conducting cells of vascular plants also have complexly sculpted secondary wall thickenings that reinforce the primary walls and are impregnated with the polyphenolic polymer lignin. These vascular cells, comprising the xylem tissue, are typically responsible both for water transport and structural support in the plant — wood is an example.

Vascular cells are dead at maturity and can only physiologically interact with the rest of the organism through their cell walls. The distribution of hydrophilic polysaccharides and hydrophobic lignin within individual cell-wall layers may greatly influence the cells' structural and transport properties. For example, lignin would be optimally placed in the primary wall and middle la-

mella layer between adjacent cells in order to maximize the cell adhesion necessary for structural support, but such placement may interfere with aspects of hydraulic function as discussed below. Despite the functional importance of cell walls, details of their composition are difficult to observe due to the submicron scale of cell-wall layering. X-ray microscopy at the NSLS has allowed us to document the detailed distribution of wall polymers and demonstrate that sites of lignin deposition within

cell walls vary substantially across vascular plants (**Figure 1**).

It was previously discovered that the resistance properties of xylem can be reversibly modified by altering the ionic concentration of the water being transported. The mechanism proposed for this was that the pectin in the middle lamella layer acts as a hydrogel and reversibly contracts and expands due to the binding and release of ions from solution, thereby altering the size of the pores through which

water travels from one xylem cell to the next. We hypothesized that the lignification of the middle lamella, which provides structural support, would disrupt this capacity to modify the xylem's transport-resistance properties. We then demonstrated that, in fact, patterns of lignin deposition and resistance properties are strongly correlated (**Figures 1 & 2**).

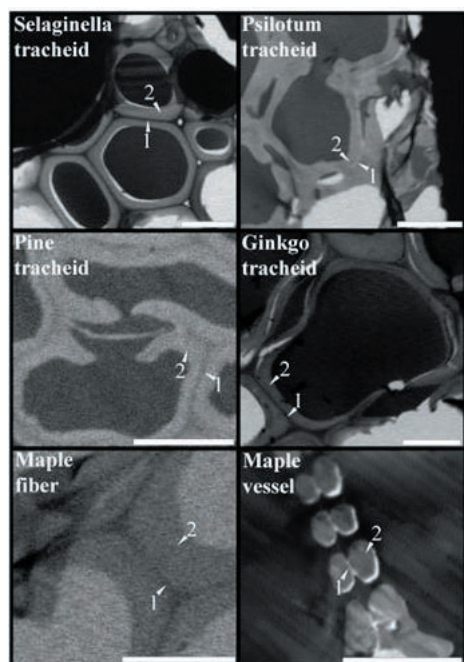


Authors (from left): Kevin Boyce, Missy Holbrook, Maciej Zwieniecki, and George Cody

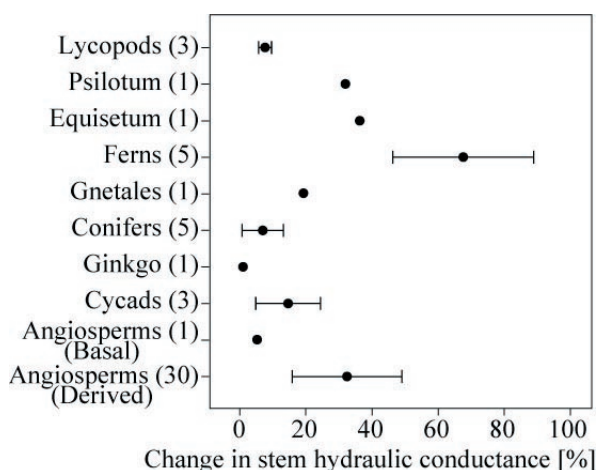
This work suggests that a number of important evolutionary trends in vascular cells that have been traditionally framed in terms of changes in cell shape and wall anatomy must also be considered in terms of the evolution of wall chemistry, including the diversification of vascular cell types. For example, the primitive condition in vascular plants

is to have a single cell type (tracheids) responsible for both support and transport, but flowering plants have evolved morphologically distinct cell types specialized either for transport (vessels) or for support (fibers). This appears also to involve a divergence in patterns of lignin deposition. Vessels have a lignification pattern that might

compromise structural support, but fibers that maintain an alternative lignification pattern are available to provide that support (**Figure 1**). It is likely that a number of such shifts in wall biochemistry may be documented through further studies of living and fossil plants.



**Figure 1.** X-ray microscopy images of xylem cells, with darker shades indicating greater x-ray absorbance and lignin abundance. Images were taken at 285.2-286 eV absorption peak for aromatic carbon, which is most prevalent in lignin. All of the images depict cross-sections of xylem cells: water conducting tracheids and vessels, or non-conducting fibers specialized for support. *Selaginella* and *Psilotum* are basal vascular plants with a fern-grade organization. *Maple* is a flowering plant. Primary walls (1) and secondary walls (2) are labeled in each image. Nearly black or white areas found in cell lumens are epoxy or holes in the section. Scale bars are 6 microns.



**Figure 2.** Percent increase of stem hydraulic conductance (mean ± standard deviation) measured with 20 mMol KCl solution over conductance determined with deionized water. Numbers in parentheses reflect the number of different species used in the analysis.